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The Reproductive Cycles of the Intertidal Bivalves *Crassostrea cucullata* (Born, 1778) and *Perna perna* (Linnaeus, 1758) from the Transkei Coast, Southern Africa

by

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Abstract. Histological analysis was used to determine the reproductive cycles of the rock oyster *Crassostrea cucullata* and the brown mussel *Perna perna* from the Transkei coast, Southern Africa. Gametogenesis in *C. cucullata* took place between August and January, and spawning occurred in late summer (February to March), after which time, the animals became inactive and of indeterminate sex until the cycle recommenced. The observed cycle is compared with that described in tropical and temperate regions. *Perna perna* has an extended breeding season characterized by low levels of asynchronous, intermittent spawning between February and September. It is suggested that such a reproductive cycle may be an adaptive strategy to ensure survival of some larvae in their unpredictable "upwelling" environment.

INTRODUCTION

Numerous studies have been carried out on the reproductive cycles and spawning of bivalves (see Andrews, 1979, and Sastry, 1979, for reviews). However, relatively little is known of the reproductive cycles of South African bivalves. The only notable studies are those of De Villiers (1973) on *Donax serra* and Griffiths (1977) on *Aulacomya ater* and *Choromytilus meridionalis*. This paper describes the reproductive cycles of two intertidal bivalves, abundant on the Transkei coast: the rock oyster *Crassostrea cucullata* and the brown mussel *Perna perna*.

The rock oyster *Crassostrea cucullata* forms conspicuous bands on rocks in the upper balanoid zone. It is Indo-Pacific in origin, ranging from East Africa to the Pacific islands (Braley, 1982). The reproductive biology of *C. cucullata* has not been studied previously in Southern Africa. However, elsewhere this species has received considerable attention because of its cultivation potential. Information on the reproduction of *C. cucullata* is available from Australia (Roughley, 1933), Guam (Braley, 1982), Pakistan (Asif, 1980), India (Nagabhushanam & Bidarkar, 1977), Singapore (Ling, 1970), and East Africa (Van Someren & Whitehead, 1961).

Perna perna is widely distributed in tropical and subtropical regions of the Indo-Atlantic (Siddall, 1980). On the east coast of Africa it has been recorded from central Mozambique around to False Bay in the Cape (Kilburn & Rippey, 1982). It is usually associated with wave-exposed situations, often forming dense aggregations on rocky shores from the lower balanoid zone down to 5 m below chart datum (Berry, 1978). A brief description of the spawning periods of *P. perna* on the subtropical Natal coast, just north of Transkei, is given by Berry (1978). Information is also available on the reproduction of *P. perna* from the Congo (Cayre, 1981) and Venezuela (Velez & Martinez, 1967; Carvajal, 1969; Velez, 1971).

MATERIALS AND METHODS

At monthly intervals, between August 1982 and September 1983, specimens of *Crassostrea cucullata* and *Perna perna* were collected from the shore at Hluleka (31°49′S, 29°19′E). All collections were made at spring low tide and random samples of 20 to 30 individuals were taken. Gonadal tissue from the mid-region of the mantle lobe was removed and fixed in either Bouin's or 10% formol-saline

Table 1

Distribution of gonad stages in samples of *Crassostrea cucullata* from Hluleka, Transkei (n = sample size; GI = gonad index; d_1 to d_5, r, and s are developmental stages).

		Number of individuals at each stage														
		Male							Female							
Date	n	d_1	d_2	d_3	d_4	d_5	r	sp	d_1	d_2	d_3	d_4	d_5	r	sp	in	GI
Aug 1982	21	3		1	1			1	1						3	11	0.71
Sept	26		1	7	4				1	9	3					1	2.58
Oct	26		1	5	4					1	10	4				1	3.12
Nov	26		1	2	8					1	6	8					3.54
Dec	30	2	1	4	10	3	1	1				3	5				3.73
Jan 1983	25				4	9						2	8	1		1	4.48
Feb	24				1	4	9						1	8	1		3.38
Mar	24					1	15							6	2		2.29
Apr	23					1	3	9							5	5	1.22
May	23						2	10	1						1	9	0.74
June	24						1	16							2	5	0.79
July	18	1			1		2	3	3			1	1		2	4	1.56
Aug	23	1	8	1	1			2	4	1	4					1	1.91
Sept	19		1	3	4					1	4	6					3.42

prior to routine preparation for histological studies. The embedded material was sectioned at 7 μm, and then stained with Delafield's haematoxylin and eosin.

The sectioned material was examined microscopically and subjectively allocated a maturity index based on the differing proportions of the various gametogenic cells present. The classification scheme adopted here is a modification of that used by SEED (1969). Four main stages in the annual cycle can be recognized: inactive (in), developing (d), spawning (r), and spent (sp). The "developing" stage is further divided into five sub-stages—d_1, d_2, d_3, d_4, and d_5—which reflect the progression of gametogenesis. For each monthly sample the mean gonad index (GI) was determined by multiplying the number of individuals at each stage by a factor representing the arbitrary rating of the stage. The sum of these products was then divided by the total number of individuals in the sample. The gametogenic stages were assigned ratings as follows: stage $d_1 = 1$, $d_2 = 2$, $d_3 = 3$, $d_4 = 4$, $d_5 = 5$, r = 3, sp = 1, and in = 0.

RESULTS

Crassostrea cucullata

Only three instances of hermaphroditism were noted among the 333 oysters sectioned. Two of these revealed occasional oocytes among the spermatogenic cells at the edge of the follicles. Both male and female gametes were evident in the other hermaphrodite; the oocytes were attached to the follicle wall and spermatozoa were restricted to the lumen. The oysters examined were within the 20 to 80 mm size range. No differences were found in the size distributions of males and females. The only deviations from a 1:1 sex ratio were those associated with the occurrence of oysters of indeterminate sex in May and June 1983.

Increases in the gonad index from August 1982 to January 1983 and from June 1983 to the cessation of sampling in September 1983 marked periods of gametogenic development. Spawning appeared to take place between February and May 1983, as indicated by the declining gonad index (Table 1). Throughout most of the reproductive cycle, the development of male *Crassostrea cucullata* paralleled that of females. Inactive oysters of indeterminate sex were prevalent in August 1982 and from April to July 1983. The occurrence of individuals at various developmental stages each month indicated a lack of gametogenic synchrony. Spawning oysters (stage r) constituted over 40% of the population between February and March. Animals in this state were recorded up to July. There was no evidence of redevelopment during the spawning period.

Perna perna

The sexes are separate, and no hermaphrodites were found. At maturity, females could be distinguished by the orange coloration of the mantle tissue, compared to the white mantles of males. At the beginning of the reproductive cycle, such visual observations were often misleading. Resting animals, in which connective tissue filled the mantle, were easily confused with mature males. Of the 307 mussels sectioned, 142 were male, 133 female, and 32 of indeterminate sex. There were no significant departures from the expected 1:1 sex ratio ($P < 0.05$). Mussels examined were between 20 and 70 mm total length. Parasitic infestation by digenean trematode larvae was prevalent, sometimes resulting in parasitic castration.

Table 2

Distribution of gonad stages in samples of *Perna perna* from Hluleka, Transkei (n = sample size; GI = gonad index; d_1 to d_5, r, and s are developmental stages).

		Number of individuals at each stage															
		Male							Female								
Date	n	d_1	d_2	d_3	d_4	d_5	r	sp	d_1	d_2	d_3	d_4	d_5	r	sp	in	GI
Aug 1982	22			3	3	4	2				1	3	1	4	1		3.64
Sept	19					2	9		3						2	3	1.05
Oct	22	2	2	4		3			2	1	2				1	5	1.55
Nov	26	2		2	4		1		2	2	3					10	1.73
Dec	27	2	2	4	1					6	5				2	5	1.89
Jan 1983	19			2	5	1			1	2	2		1			5	2.47
Feb	28		2	2	7	2	1		1	1	2	5	4	1			3.68
Mar	20		2	6	2					3	4	3					3.00
Apr	26				7	1	4				1	4	5	4			3.50
May	22				1	7	3					1	7	3			4.36
June	21				2		8				2			8		1	2.95
July	20				2	6	4						7	1			4.40
Aug	13				1	1	1					1	7	1		1	4.15
Sept	22	1	1	4	2		2			2	1	2	1	2	2	2	2.59

There was a gradual increase in the gonad index between September 1982 and February 1983, indicating gametogenic development (Table 2). The presence of animals at several developmental stages in the monthly samples indicated asynchronous development. The development of male *Perna perna* generally paralleled that of the females. Decreased gonad index values in March, June, and September may be indicative of spawning activity. However, reference to data on the distribution of gonad stages indicated that only developing individuals at stages d_2, d_3, and d_4 were present in the March sample. It is therefore suggested that the decline in gonad index at this time does not reflect spawning but is rather associated with the regeneration of sexual products following a partial spawning in February. Between April and July over 20% of the mussels examined were in spawning condition, characterized by partially empty gonadal follicles. In some cases further gametogenesis was evident, which lends support to the suggestion that *P. perna* is a partial spawner. Spent mussels, with residual gametes present in the follicles, were relatively scarce. Mussels of indeterminate sex, apparently in a resting state, constituted more than 20% of the population between October and January.

DISCUSSION

Studies on the reproductive cycle of *Crassostrea cucullata* have been completed at seven locations (Table 3). Continuous reproductive activity is reported in the tropical populations (Awati & Rai, 1931; Ling, 1970; Nagabhushanam & Bidarkar, 1977; Asif, 1980; Braley, 1982). Despite some asynchrony, temperate populations of *C. cucullata* and its recognized subspecies (Roughley, 1933; Dinamani, 1974; Lasiak, this study) have a single annual reproductive cycle. This follows the general trend shown by other oysters of the genus *Crassostrea* in temperate latitudes; spawning takes place in summer and animals enter a regressed or inactive phase during the colder months (Loosanoff, 1942; Kennedy & Battle, 1964; Galtsoff, 1964; Berg, 1969).

Differences in the periods of gametogenesis and breeding activity have been recorded in geographically separated populations of various bivalve species (Sastry, 1979). The reproductive cycles of latitudinally separated populations of *Crassostrea cucullata* follow the temperature-latitude zoogeographic principle outlined by Thorson (1946). That is, tropical and subtropical species are expected to spawn earlier and over a more extended period than their counterparts at the poleward limits of their distribution. Sastry (1970) proposed that variations of this kind represent adaptive responses to geographic differences in temperature and food production. Although the gonadal cycle of *C. cucullata* in temperate waters appears to be linked to seasonal temperature patterns, temperature does not regulate gametogenesis in tropical populations. Several workers (Ling, 1970; Nagabhushanam & Bidarkar, 1977; Stephen & Shetty, 1981) have shown that reduction in salinity, associated with heavy monsoon rains, acts as a trigger initiating spawning in some populations of *C. cucullata*. However, Braley (1982) was unable to correlate spawning activity of *C. cucullata* from Guam with environmental perturbations in water temperature, salinity, turbidity, or climate. The continuous spawning activity of the latter population may result from a lack of exogenous cues for spawning, as suggested by Giese & Pearse (1974).

The reproductive cycle of the brown mussel *Perna per-*

Table 3

Geographic location and reproductive cycle of *Crassostrea cucullata.*

Location	Latitude	Reproductive cycle	Source
Singapore	2°S	Continuous, three peaks after monsoons	Ling (1970)
Guam	13°S	Gametogenic cycle 3–4 months long. Spawning continuous, three major peaks, Nov–Dec, Mar–April, and late June	Braley (1982)
Ratnagiri, India	17°S	Gametogenesis from February onward; all ripe by July but no spawning until after monsoon. Spawning from late September to January	Nagabhushanam & Bidarkar (1977)
Bombay, India	19°S	Continuous, except for monsoon periods	Awati & Rai (1931)
Karachi, Pakistan	25°S	Continuous with three peaks, Jan, May, and Oct–Nov	Asif (1980)
Hluleka, Transkei	32°S	Gametogenesis begins in July–Aug and reaches maximum development in November. Major spawning Feb–Mar	Lasiak, this study
Sydney, Australia	34°S	Summer spawning extending to April–May	Roughley (1933)

na does not conform to the sequence expected for tropical species near the poleward limits of their distribution. Fluctuations in the gonad index indicate that *P. perna* on the Transkei coast has an extended breeding season characterized by low levels of spawning activity from February to September. Two well-defined spawning peaks in winter (May to August) and spring (September to October) have been described in *P. perna* from the Natal coast (Berry, 1978). However, Berry also noted that spawning activity tended to take place over an extended period, with 25% of the population breeding for three to six months of the year. Asynchronous, intermittent spawning has also been reported in two mussels, *Aulacomya ater* and *Choromytilus meridionalis,* on the west coast of Southern Africa (Griffiths, 1977). A protracted breeding season has also been recorded for *P. perna* from Venezuela (Velez & Martinez, 1967; Carvajal, 1969; Velez, 1971) (Table 4).

Spawning and larval settlement of *Perna perna* have been linked to periods of lower surface water temperature, intense winds, and maximum upwelling (Velez & Martinez, 1967; Carvajal, 1969; Acuna, 1977; Cayre, 1981). No information is available on temporal fluctuations in environmental parameters or food availability off the Transkei coast during the course of this study. However, incursions of cold water, associated with upwelling, are known to occur in this area, particularly in the winter (Macnae, 1962). Although it is difficult to demonstrate a causal relationship between temperature and reproductive activity, it is probable that either a threshold temperature or a rate of change in temperature influences gametogenesis and acts as a cue for spawning (Sastry, 1979). Velez & Epifanio (1981) have shown that gametogenesis in *P. perna* is inhibited by high temperatures. Both Carvajal (1969) and Lunetta (1969) found spawning of *P. perna* to occur when sea temperature dropped from 28 to 22°C. Upward temperature shocks have also been used to induce spawning in this mussel (Siddall, 1980).

Bayne (1976) has discussed the need to coordinate the time of spawning so that larvae and adults have access to abundant food supplies. Such a strategy should maximize the probability of successful recruitment. Griffiths (1977) has proposed that, in upwelling areas, spawning in response to the rate of change in temperature ensures that larvae will be produced at a time when phytoplankton

Table 4

Geographic location and reproductive cycle of *Perna perna.*

Location	Latitude	Reproductive cycle	Source
Sucre, Venezuela	10°S	Continuous, peak activity January to April	Velez & Martinez (1967)
		Three peaks in condition index indicating spawning from October to January, February to April, and from July to August	Velez (1971)
		Three periods of intense spawning activity: September to December, February, and April to June	Carvajal (1969)
Congo	4°S	Two spawning seasons: June to September and December	Cayre (1981)
Natal, South Africa	30°S	Two spawning peaks: first, always the greatest, between May and August, with second peak in spring, September to October	Berry (1978)
Hluleka, Transkei	32°S	Protracted spawning with major peak April to July	Lasiak, this study

availability is enhanced. Asynchronous intermittent spawning may be an adaptation to life in the unpredictable environment characteristic of upwelling areas. As NEWELL *et al.* (1982) have pointed out, continuous dribble spawning ensures that in the face of some catastrophic event, which could kill or prevent settlement of larvae, only a small proportion of potential recruits would be lost. More frequent sampling coupled with continuous environmental monitoring is needed to clarify the apparent relationship between temperature change and spawning activity in the mussel *Perna perna*.

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